Alterations of electrophysiological correlates of performance monitoring with age

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von

Dipl.-Psych. Melanie Schreiber

Prof. Dr. Jan-Hendrik Olbertz

(Präsident der Humboldt-Universität zu Berlin)

Prof. Dr. Elmar Kulke

(Dekan der Mathematisch-Naturwissenschaftlichen Fakultät II)

Gutachter/Gutachterinnen

1. Prof. Dr. Norbert Kathmann
2. Prof. Dr. Birgit Stürmer
3. Prof. Dr. Michael Falkenstein

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Summary

Executive functions decline with increasing age and a growing body of research aims at investigating age-related changes of the underlying processes. One important function is to monitor actions and action outcomes, which is necessary for flexible adjustments and learning. This so-called performance monitoring can be measured with event-related potentials (ERP), namely the error-related negativity/error negativity (ERN/Ne) and the correct response-related negativity/correct negativity (CRN). In this work performance monitoring in younger and older adults is examined in three different tasks with the aim to advance knowledge about potential compensatory strategies in the older age group and their implications for ERP results. Findings revealed reduced ERN/Ne amplitudes and larger or similar-sized CRN amplitudes in older compared to younger adults. While only younger adults showed a decrease of ERN/Ne with higher task difficulty, both age groups showed a reduction of ERN/Ne in the speed compared to the accuracy condition. Additionally, younger adults showed variations, in that the CRN was smaller for compatible compared to incompatible trials, in the easy compared to the difficult condition, and in the speed compared to the accuracy condition. Conversely, CRN amplitudes in older adults did not vary with conditions and did not differ from ERN/Ne amplitudes. Behaviorally, older adults committed less errors and showed longer response latencies compared to younger adults. This behavioral pattern may reflect compensatory or strategic adjustments with age which may be due to deficits in the use of a successful combination of proactive and reactive control. It was further assumed that ERN/Ne and CRN share a common process that reflects general monitoring functions and the ERN/Ne includes an additional process that reflects error-specific monitoring. Accordingly, the ERN/Ne attenuation in older adults is either caused by reduced error-specific processing or compromised general monitoring functions. Age-related changes in ERP findings could indicate altered engagement of compensatory cognitive control in older compared to younger adults. However, this question has to be further clarified in future studies.

Zusammenfassung

Exekutive Funktionen sind mit dem Alter reduziert und mit zunehmendem Interesse widmet sich die Forschung der Untersuchung der zugrunde liegenden Prozesse dieser altersbezogenen Veränderungen. Handlungen und deren Konsequenzen zu überwachen ist eine notwendige Funktion für eine flexible Anpassung und für das Lernen. Die so genannte Handlungsüberwachung kann mit ereigniskorrelierten Potentialen (EKP) wie der error-related negativity/error negativity (ERN/Ne) und der correct response-related negativity/ correct negativity (CRN) gemessen werden. Diese Arbeit untersucht die Handlungsüberwachung bei jüngeren und älteren Erwachsenen an Hand drei verschiedener Aufgaben mit dem Ziel, das Wissen über potentielle kompensatorische Strategien bei Älteren und deren Auswirkung auf die EKP Befunde zu erweitern. Die Ergebnisse zeigten reduzierte ERN/Ne und größere oder vergleichbar große CRN Amplituden bei Älteren im Vergleich zu Jüngeren. Während nur die Jüngeren eine Reduktion der ERN/Ne mit größerer Aufgabenschwierigkeit zeigten, zeigten beide Altersgruppen eine ERN/Ne Reduktion unter der Instruktion, die Geschwindigkeit anstatt Genauigkeit erforderte. Darüber hinaus zeigten die Jüngeren kleinere CRN Amplituden bei kompatiblen als bei inkompatiblen Trials, in der leichten als in der schweren Bedingung und in der Geschwindigkeits- als in der Genauigkeitsbedingung. Im Unterschied dazu zeigte sich keine CRN Variation bei Älteren und CRN Amplituden unterschieden sich nicht von ERN/Ne Amplituden. Auf Verhaltensebene waren Ältere durch geringere Fehlerraten und längere Reaktionszeiten im Vergleich zu Jüngeren gekennzeichnet. Dieses Verhaltensmuster deutet möglicherweise auf eine kompensatorische oder strategische Anpassung in Folge von Defiziten in der Nutzung einer erfolgreichen Kombination von proaktiver und reaktiver Kontrolle hin. Darüber hinaus wird davon ausgegangen, dass ERN/Ne und CRN einen gemeinsamen Prozess darstellen, der allgemeine Überwachungsfunktionen reflektiert. Die ERN/Ne beinhaltet zusätzlich einen Prozess, der Fehlerüberwachung signalisiert. Daraus ergibt sich die Vermutung, dass die reduzierte ERN/Ne bei Älteren entweder auf eine Verringerung spezifischer Fehlerprozesse oder auf eine Beeinträchtigung allgemeiner Überwachungsfunktionen zurückzuführen ist. Altersbezogene Veränderungen der EKP Befunde könnten den veränderten Einsatz von kompensatorischer Kontrolle bei Älteren im Vergleich zu Jüngeren reflektieren. Dieser Frage sollte in zukünftigen Studien nachgegangen werden.

1. Introduction and theoretical background of performance monitoring

It is well known that executive functions decline during aging (Salthouse, Atkinson, & Berish, 2003; Treitz, Heyder, & Daum, 2007; West, 1996). Accordingly, performance monitoring which is a part of executive functions is assumed to be altered with age. But, processes that are responsible for age-related alterations in performance monitoring are still not comprehensively understood. The function of performance monitoring is assumed to be reflected by components of the event-related brain potential (ERP). The aim of the present work was to further clarify performance monitoring alterations with age. To this end, three studies were conducted and ERP components in different tasks were compared between younger and older adults.

In daily life it is necessary to pay attention to the current action and to notice any mismatch of the intention and the actual outcome that appears during performance. As soon as a mistake is detected, one has to interrupt the task to correct the mistake. Thus, goal-directed acting requires monitoring of behavior. This process constitutes performance monitoring for which activity in the anterior cingulate cortex (ACC) plays a crucial role (Bush, Luu, & Posner, 2000; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004a). Performance monitoring includes the assessment and comparison of actions and their outcomes with action goals. It provides the indication of whether behavior should be adjusted and improved. Therefore, error monitoring plays a pivotal role for goal-directed behavior, flexible performance adaptation, and acquirement of new behavior (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004b).

On the behavioral level, performance monitoring is reflected by the consequences resulting from errors, feedback evaluation, and conditions, in which action outcome is related to response uncertainty or response conflict. Behavioral adjustments appear most obvious when errors are immediately corrected even if it is not instructed (Rabbitt, 1966). A strategic adjustment process is also reflected in post-error slowing which is the delayed latency of correct reactions after error commission (Rabbitt, 1966). A further adjustment process is post-error reduction of interference characterized by the reduction of response time differences between compatible and incompatible trials after error commission (Ridderinkhof et al., 2002). This can result in lower error rates subsequent to an error.

Although these processes are assumed to reflect behavioral adjustments, error detection may also interfere with subsequent performance (Fiehler, Ullsperger, & von Cramon, 2005; Rabbitt & Rodgers, 1977).

An ERP component that is related to performance monitoring processes is the error negativity (Ne, Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990) or error-related negativity (ERN, Gehring, Goss, Coles, & Meyer, 1993). The ERN/Ne presents as a negative ERP component approximately 50-100 ms following erroneous responses. It has been observed in various tasks that employ a variety of stimulus and response modalities (Bernstein, Scheffers, & Coles, 1995; Holroyd, Dien, & Coles, 1998; Van 't Ent & Apkarian, 1999) and task difficulty levels (Band & Kok, 2000; Mathalon et al., 2003a; Mathewson, Dywan, & Segalowitz, 2005; Moser, Hajcak, & Simons, 2005; Themanson, Hillman, & Curtin, 2006). The ERN/Ne is not only detected in response choice errors but also in failed inhibition errors (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Mathalon, Whitfield, & Ford, 2003b). It is typically measured at midline frontal or central electrode sites where it is largest (i.e., FCz). The ACC, or more specifically, a source in the rostral cingulate zone, was identified as the most plausible generator of the ERN/Ne according to several studies using source localization (Dehaene, Posner, & Tucker, 1994; Holroyd et al., 1998; van Veen & Carter, 2002), intracerebral recording (Brazdil, Roman, Daniel, & Rektor, 2005), and combined recordings from electroencephalogram and functional magnetic resonance imaging (Debener et al. 2005). In line with that notion, decreased ERN/Ne amplitudes were found in patients with ACC lesions (Stemmer, Segalowitz, Dywan, Panisset, & Melmed, 2004). Examinations with patients suffering from focal brain lesions point to the involvement of further brain structures like the lateral prefrontal cortex (Gehring & Willoughby, 2002; Ullsperger & von Cramon, 2006b; Ullsperger, von Cramon, & Müller, 2002). Moreover, the dopaminergic neurotransmitter system seems to be crucial for the appearance of the ERN/Ne (de Bruijn, Hulstijn, Verkes, Ruigt, & Sabbe, 2004; de Bruijn, Sabbe, Hulstijn, Ruigt, & Verkes, 2006; Holroyd & Coles, 2002).

The ERN/Ne was found to be larger when error rates were low (Gehring et al., 1993; Hajcak, McDonald, & Simons, 2003; but see Falkenstein et al., 2000) indicating that errors are more salient in case of infrequent errors. Some studies observed increased ERN/Ne amplitudes with increased post-error slowing (Debener et al., 2005; Gehring et al., 1993; Scheffers, Humphrey, Stanny, Kramer, & Coles, 1999). This finding supports the assumption of the ERN/Ne to be a signal indicating the need for behavioral adjustment (Ridderinkhof et al., 2004a; Ullsperger, Volz, & von Cramon, 2004; Ullsperger & von Cramon, 2006a). However, other studies did not find this relation (Gehring & Fencsik, 2001; Hajcak et al., 2003; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). Post-error slowing was found to be reduced in misperceived errors compared to perceived errors whereas ERN/Ne amplitudes did not differ with error awareness (Endrass, Reuter, & Kathmann, 2007; Nieuwenhuis et al., 2001). This finding indicates that, in contrast to the ERN/Ne, post-error slowing depends on error awareness. Moreover, it is independent from the ERN/Ne. Finally, the ERN/Ne was reduced when participants responded under time pressure whereas it was enhanced when participants focused on response accuracy (Falkenstein et al., 1990; Gehring et al., 1993).

Interestingly, a negative deflection with a similar topography as the ERN/Ne has been detected on correct responses (Falkenstein et al., 2000; Ford, 1999; Gehring & Knight, 2000; Scheffers & Coles, 2000; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000). This “Ne-like” component has also been referred to as correct (response-related) negativity (Nc/CRN, Falkenstein et al., 2000; Ford, 1999). Although results about the source of the CRN are less consistent it has also been localized in the ACC (Suchan, Zoppelt, & Daum, 2003) or frontal brain regions (Mathalon et al., 2003a). Most studies found smaller CRN than ERN/Ne amplitudes (Beste, Willemssen, Saft, & Falkenstein, 2009; Falkenstein, Hoormann, & Hohnsbein, 2001b; Mathalon et al., 2003a; Nessler, Friedman, Johnson, & Bersick, 2007). Furthermore, there is evidence for the assumption that both components differ functionally (Endrass, Klawohn, Gruetzmann, Ischebeck, & Kathmann, 2012a). One supporting finding is that the ERN/Ne varied with the monetary value of trials whereas the CRN did not change (Hajcak, Moser, Yeung, & Simons, 2005).

There is an ongoing debate about the functional role of the ERN/Ne. The most prominent accounts include the assumptions that it reflects error detection (e.g., Bernstein et al., 1995; Falkenstein et al., 1990; Falkenstein et al., 2000; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996), a reinforcement learning signal (e.g., Holroyd & Coles, 2002), response conflict (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001; Yeung, Cohen, & Botvinick, 2004), or an emotional or motivational response to errors (Bush et al., 2000; Gehring & Willoughby, 2002; Pailing, Segalowitz, Dywan, & Davies, 2002). Overall, the ERN/Ne is viewed as a monitoring signal that indicates the need for adjustment of cognitive control to prevent future errors (Ridderinkhof et al., 2004a). The CRN is discussed controversially, as it challenges the view of response-related activity to be error-specific. Explanations for the CRN comprise the assumptions of a response comparison process (Falkenstein et al., 2000; Vidal et al., 2000), an emotional reaction (Luu, Collins, & Tucker, 2000), response uncertainty (Coles, Scheffers, & Holroyd, 2001; Pailing & Segalowitz, 2004a), or a co-activation of correct and incorrect responses (Luu, Flaisch, & Tucker, 2000; Scheffers et al., 1996; Vidal et al., 2000). Furthermore, the CRN might be a signal for an inadequate response strategy (Bartholow et al., 2005).

Originally, the ERN/Ne was considered as a correlate of the error detection process. It occurs when a mismatch between the representation of the required response (correct, intended) and the actual response (incorrect, not intended) is detected (Bernstein et al., 1995; Coles et al., 2001; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991). Accordingly, several studies showed that the ERN/Ne is larger when the correct response and the incorrect response are more dissimilar (Bernstein et al., 1995; Falkenstein, Hohnsbein, & Hoormann, 1994; Scheffers et al., 1996; but see Gehring & Fencsik, 2001). Since the error detection account was challenged by the presence of the CRN, it was alternatively suggested that the ERN/Ne does not reflect the error detection signal but the comparison process between the required and the actual response and this is also existent during correct responses (Vidal, Burle, Bonnet, Grapperon, & Hasbroucq, 2003; Vidal et al., 2000).

The reinforcement learning theory of the ERN/Ne (RL theory; Holroyd & Coles, 2002) is partially based on the mismatch theory. It was proposed that the basal ganglia monitor external as well as internal information to evaluate on-going events built on learned expectations (Holroyd & Coles, 2002). The performance outcome, i.e., the occurrence of rewards or negative events such as losses or negative feedback, provokes the basal ganglia to induce an increase or a decrease in phasic midbrain dopamine activity (e.g., Schultz, 2002, 2007). The ERN/Ne results from a decrease of midbrain dopamine levels that leads to a disinhibition of the ACC. This may indicate that events are worse than expected. Error signals serve to predict future rewards and non-rewards and to adapt future behavior; thereby playing a pivotal role for learning (Barto, 1995; Montague, Dayan, & Sejnowski, 1996; Schultz, 2002).

The conflict monitoring theory considers the ERN/Ne as a conflict signal between two or more simultaneously active incompatible responses. Consistently, response-related negativities should be observed on incorrect as well as on correct responses, since both representations may be activated during continued stimulus processing (Yeung et al., 2004). From this point of view, the ACC should be active on error trials as well as on correct trials that elicit high response conflict. In fact, ACC activity was obtained for incompatible trials (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 1998; Carter et al., 2000).

In contrast to these cognitive accounts on the function of the ERN/Ne, it was also suggested that the ERN/Ne could reflect emotional or motivational processes following error commission. This account is supported by the finding of individual differences in performance monitoring (Pailing & Segalowitz, 2004b) and the sensitivity of the ERN/Ne to error significance (Gehring et al., 1993).

Finally, the question whether ERN/Ne and CRN reflect similar or different processes was addressed with independent component analysis (ICA) and temporospatial principal component analysis (PCA; Endrass et al., 2012a; Hoffmann & Falkenstein, 2010; Roger, Benar, Vidal, Hasbroucq, & Burle, 2010). ICA identified a single component that varied with amplitude modulations of ERN/Ne and CRN supporting the idea of a common process reflected by both ERP components. Alternatively, temporospatial PCA revealed two components, suggesting that two underlying processes are involved in performance monitoring: a common process and an error-sensitive process (Endrass et al., 2012a).

2. Age-effects on performance monitoring and behavioral performance

Age-related alterations of performance monitoring have consistently been found but the underlying mechanisms are not well understood. Structural and functional alterations in the older brain could be associated with performance monitoring and age: The prefrontal cortex (West, 1996), the dopaminergic neurotransmitter system (Backman, Nyberg, Lindenberger, Li, & Farde, 2006), and involved cognitive functions (e.g., executive functions; Rypma & D'Esposito, 2000; Volkow et al., 1998) are affected by age.

Different tasks were administered (e.g., mental rotation task, Band & Kok, 2000; four choice reaction time task and flanker task, Falkenstein et al., 2001b; source memory task, Mathalon et al., 2003a) and older adults repeatedly showed reduced ERN/Ne amplitudes compared to younger adults (Band & Kok, 2000; Falkenstein et al., 2001b; Mathalon et al., 2003a; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Themanson et al., 2006; West, 2004). However, recent studies did not replicate the ERN/Ne reduction in (probabilistic) learning tasks (Eppinger, Kray, Mock, & Mecklinger, 2008; Pietschmann, Endrass, Czerwon, & Kathmann, 2011a; Pietschmann, Endrass, & Kathmann, 2011b; Pietschmann, Simon, Endrass, & Kathmann, 2008) which might be due to the specific task characteristics. The smaller ERN/Ne in older adults is suggested to arise from a limited ability to detect errors and consequences have to be most obvious in more difficult tasks (Band & Kok, 2000). In fact, the finding of reduced ERN/Ne amplitudes in older adults performing a flanker interference task (Falkenstein et al., 2001a; Mathewson et al., 2005; Nieuwenhuis et al., 2002) indicates that error monitoring is already altered in simple choice reaction time tasks. This leads to the assumption of a more basal deficit in the older age group. A potential candidate for this basal deficit is a decreased dopaminergic functioning (Nieuwenhuis et al., 2002). Evidence for a relation between reduced dopaminergic functioning and attenuated ERN/Ne amplitudes has been found in pharmacological studies. Haloperidol, which is an antagonist of dopamine and inhibits receptors of dopamine, led to a reduced ERN/Ne (de Bruijn et al., 2006; Zirnheld et al., 2004).

The examination of CRN amplitudes is valuable and essential to advance knowledge about performance monitoring alterations with increasing age. But, in contrast to the ERN/Ne, only few studies examined CRN alterations with age and results on age differences are inconsistent. The CRN was found to be reduced in older compared to younger adults when performing a four-alternative reaction time task (Kolev, Falkenstein, & Yordanova, 2005) or a picture-name verification task (Mathalon et al., 2003a). Conversely, older adults showed larger CRN amplitudes in (probabilistic) learning tasks (Eppinger et al., 2008; Pietschmann et al., 2011b; Pietschmann et al., 2008). Accordingly, a CRN was only detected in the group of older adults but not in younger adults when performing a mental rotation task (Band & Kok, 2000). Another finding is that CRN amplitudes did not change with age in a four-alternative reaction time task, in a flanker interference task (Falkenstein et al., 2001b), and in a go nogo flanker task (Beste et al., 2009). While in younger adults the CRN was larger for incompatible trials than for compatible trials, it did not vary with trial compatibility in older adults (Eppinger, Kray, Mecklinger, & John, 2007; Kray, Eppinger, & Mecklinger, 2005). Together with the finding of similar-sized ERN/Ne and CRN amplitudes in the older age group (Band & Kok, 2000; Kolev et al., 2005; Pietschmann et al., 2011a; Pietschmann et al., 2011b; Pietschmann et al., 2008) this may indicate that older adults have deficits to successfully adjust behavior to the changing task context (Eppinger et al., 2007).

Noteworthy, age-related changes in ERP correlates are not necessarily accompanied by poor behavioral adaptation. Rabbit (1979) was one of the first who investigated behavioral correlates of performance monitoring and their changes with age. He showed that younger and older adults neither differed in error correction (Rabbitt, 1979, 1990, 2002) nor in post-error slowing (Rabbitt, 1990). These findings are confirmed by more recent studies showing that error (correction) rates and post-error slowing were not affected by age (Band & Kok, 2000; Falkenstein et al., 2001b; Gehring & Knight, 2000; Mathalon et al., 2003a; Nieuwenhuis et al., 2002). Rabbitt (1979) concluded that error monitoring is intact in the older age group. In contrast, ERP studies show a deficit of performance monitoring in older adults. Impaired ERP correlates of error processing but intact behavioral measures are difficult to explain. Diverging results may occur because deficits in older adults are too weak to be reflected in behavioral measures (Falkenstein et al., 2001b) or older adults recruit compensatory processes to overcome their deficits (Band, Ridderinkhof, & Segalowitz, 2002).

Probably the most reliable behavioral difference between younger and older adults is a slowing of response times in older adults (Band & Kok, 2000; Birren & Fisher, 1995; Falkenstein et al., 2001b; Hoffmann & Falkenstein, 2011; Kolev et al., 2005; Mathalon et al., 2003a; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Rabbitt, 2002; Salthouse, 1996). In contrast to response slowing, error rates did not differ between age groups or were smaller in older compared to younger adults. This behavioral pattern indicates that older adults focus on accuracy and reach a comparable performance to that of younger adults by the expense of slower responses (Braver & Barch, 2002; Treitz et al., 2007; Verhaeghen & Cerella, 2002; West, 1996). This more conservative and careful response strategy may be necessary to avoid errors (Hester, Fassbender, & Garavan, 2004; Rypma, Prabhakaran, Desmond, & Gabrieli, 2001; Sharp, Scott, Mehta, & Wise, 2006) since older adults exhibit deficits in multiple domains of cognitive control (Braver & Barch, 2002; Treitz et al., 2007; Verhaeghen & Cerella, 2002). Consistently, Rympa et al. (2001) reported that individuals with longer response latencies recruit more prefrontal executive control for optimal performance than individuals with shorter response latencies. Thus, this strategy is possibly not only associated with the typical behavioral pattern but also with the changes of ERN/Ne and CRN amplitudes in older adults.

Summarized, older adults show deficits in performance monitoring as indicated by reduced ERN/Ne amplitudes and changes in CRN amplitudes. Whereas behavioral performance is comparable to younger adults in terms of error rates, reaction times are prolonged in older adults. The underlying mechanism that causes performance monitoring alterations is still unclear. Among different accounts a weakened dopaminergic function (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002) and/or weakened representations of stimulus-response mappings (Nieuwenhuis et al., 2002; Pietschmann et al., 2008) seem to be interesting explanations. Empirical studies of the present thesis examined ERP and behavioral indicators of performance monitoring in younger and older adults with the aim to expand knowledge about age-related alterations and specifically to test the assumption of a relation between behavioral compensation and ERN/Ne and CRN alterations with age.

3. Empirical studies

3.1 Research objectives and overall methods

The current studies intended to specify conditions that lead to ERN/Ne and CRN alterations in older adults. We examined the potential deficit in older adults to adequately adapt to changing task demands. Thus, we investigated age-related ERN/Ne and CRN modulations with trial compatibility, task difficulty and task instruction. A further objective was to examine compensatory strategies that are possibly associated with performance monitoring alterations in the older age group.

Three studies were conducted to assess behavioral and ERP measures of younger and older adults during choice reaction time tasks. The first study focused on clarifying inconsistent CRN results in the older age group. Using trial-by-trial response accuracy ratings and force-sensitive response devices it was ensured that response uncertainty and/or partial error processing on correct trials could be controlled in the analysis of CRN amplitudes. The second study aimed at examining whether age-related alterations are associated with a reduced adaptation of performance monitoring to changing task demands. In the third study a modified flanker task with a variation of accuracy and speed instruction was used to investigate the influence of potential compensatory mechanisms on ERP components in the older age group. The main focus of the three studies was to investigate ERN/Ne and CRN amplitudes and their experimental variations between younger and older adults. We specifically intended to analyze age-related alterations of behavioral data measured by error rates, response latencies, and response accuracy ratings with the aim to examine whether and how age-related ERP differences were related to behavioral compensation in older adults.

3.2 Study 1: ERP correlates of performance monitoring in elderly

The study (Schreiber, Pietschmann, Kathmann, & Endrass, 2011) focused on the examination of potential CRN alterations with age. While ERN/Ne amplitudes were often found to be reduced in older compared to younger adults (Band & Kok, 2000; Falkenstein et al., 2001b; Mathalon et al., 2003a; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Themanson et al., 2006) CRN amplitudes were not reported or analyzed in most of the studies (e.g., Mathewson et al., 2005; Nieuwenhuis et al., 2002; Themanson et al., 2006) and results are inconsistent. In the studies analyzing the CRN, the CRN was observed to be smaller (Kolev et al., 2005), or larger (Eppinger et al., 2008; Pietschmann et al., 2011b) in older compared to younger adults, or not affected by age (Falkenstein et al., 2001b). Moreover, older adults revealed larger ERN/Ne than CRN amplitudes (Mathalon et al., 2003a) or no difference was found (Band & Kok, 2000; Pietschmann et al., 2011a; Pietschmann et al., 2011b; Pietschmann et al., 2008). While younger adults showed CRN variations with trial compatibility, older adults did not (Eppinger et al., 2007; Kray et al., 2005). Assuming that the CRN reflects the need to adapt response strategies (Bartholow et al., 2005), these findings suggest that older adults show deficits in the processing of response-related conflict and in the flexible adaptation to task demands.

Methodical issues impede the interpretation of earlier studies. First, the CRN possibly results from partial error processing on correct trials (Coles et al., 2001). With the current study responses were measured using force-sensitive response devices. This ensured the detection of subtreshold incorrect activations (i.e., partial errors) prior to correct responses and the exclusion of these trials. Additionally, error trials with partial response activation could be separated from errors with full response activation. Second, CRN amplitudes were found to be affected by response uncertainty (Pailing & Segalowitz, 2004a) leading to the assumption that the exclusion of response uncertainty is necessary to reliable measure and interpret CRN amplitudes. In the present study participants were instructed to signal subsequent to every single response whether their choice was correct, incorrect or they were uncertain regarding response accuracy. To avoid the effect of response uncertainty on ERP analyses, correct responses that were signaled to be incorrect were excluded. Consequently, response uncertainty could not have affected the CRN in the present study.

Sixteen younger adults and 16 older adults performed an arrow version of the flanker interference task (Eriksen & Eriksen, 1974; Kopp, Rist, & Mattler, 1996). Participants were asked to respond as accurately and as fast as possible in the direction the target arrow was pointing to. Flanker arrows either pointed in the same direction as the target (compatible condition) or in the opposite direction (incompatible condition). ERN/Ne amplitudes were expected to be reduced in older compared to younger adults consistent to several former studies (e.g., Falkenstein et al., 2001b). The study was designed to investigate whether the CRN is also affected by age and whether it varies with trial compatibility. While CRN amplitudes should be larger for incompatible trials than for compatible trials in younger adults, this variation should not occur in older adults (Eppinger et al., 2007; Kray et al., 2005).

ERP results showed that ERN/Ne amplitudes were smaller and CRN amplitudes were larger in older compared to younger adults. Older adults had similar-sized amplitudes for incorrect and correct responses whereas the ERN/Ne for partial errors was smaller than the CRN. In contrast, the ERN/Ne was larger than the CRN in younger adults. Trial compatibility did not affect the CRN in older adults whereas younger adults exhibited larger CRN amplitudes for incompatible than for compatible trials.

Behavioral results revealed more errors in younger than in older adults. Longer response latencies were observed for older compared to younger adults, for correct compared to incorrect trials and for incompatible correct compared to compatible correct trials. Older adults were less successful in the detection of full errors relative to younger adults while partial error detection did not differ between groups.

Group differences of ERN/Ne and CRN modulations between correct and incorrect responses as well as between compatible and incompatible correct responses suggest that younger adults adapted performance monitoring to task demands whereas older adults showed less adaptation. Decreased error-specific monitoring (reflected by ERN/Ne amplitudes) and increased general or strategic monitoring (reflected by CRN amplitudes) may indicate a dissociation of performance monitoring alterations in the older age group. As a consequence, older adults may compensate for potential deficits. The behavioral compensation is reflected by fewer errors and longer response latencies in comparison to younger adults.

3.3 Study 2: Age-effects on adjustments of performance monitoring to task difficulty

The deficit to adequately adapt to changing task demands should be reflected in behavioral and electrocortical indices when adjustments of performance monitoring and cognitive control are required. This question was addressed in the second study which assigned a visual size discrimination task with two difficulty levels (Schreiber, Endrass, Weigand, & Kathmann, 2012). ERN/Ne and CRN amplitudes were already found to vary with task difficulty (Maier, Steinhauser, & Huebner, 2010; West & Alain, 1999; Yeung, Ralph, & Nieuwenhuis, 2007). This finding was explained with response uncertainty (Pailing & Segalowitz, 2004a; Scheffers et al., 1996). It has been suggested that response uncertainty is more prominent in difficult than in easy conditions. Response uncertainty could lead to undetected erroneous responses and to correct responses that were misperceived to be incorrect. Hence, in mean amplitudes the ERN/Ne can be reduced or absent and the CRN can be enhanced during difficult task conditions. The present study employed trial-by-trial response accuracy ratings, thereby ensuring that falsely identified correct responses were excluded from computing the CRN. Thus, CRN variations did not originate from false error detection.

Data of 20 younger adults and 20 older adults were included into analyses. Two simultaneously presented dots, that were either easy or difficult to differentiate in size, appeared on the screen. Participants had to indicate as fast and as accurately as possible which one of the two dots was larger. Subsequently, participants were instructed to signal whether the response was correct, incorrect or they were uncertain regarding response accuracy. This enabled us to identify correct responses that were misperceived to be incorrect, incorrect responses that were misperceived to be correct, and correct as well as incorrect responses in which participants were uncertain. The ERN/Ne was expected to decrease and the CRN was expected to increase from the easy to the difficult condition. Assuming a deficit in the flexible adaptation to changing task demands older adults should show smaller ERP modulations with task conditions than younger adults.

Results show that in younger adults the ERN/Ne decreased and the CRN increased from the easy to the difficult condition. Consequently, ERN/Ne and CRN converged in the difficult condition, but differences between the components remained significant. Conversely, older adults did not show ERN/Ne or CRN variations with task difficulty and amplitudes were similar-sized in the easy as well as in the difficult condition. Smaller ERN/Ne amplitudes in older compared to younger adults were exclusively observed in the easy condition. CRN amplitudes did not differ between age groups.

Participants committed more errors, responded slower, and misperceived more incorrect responses in the difficult compared to the easy condition. Error rates were higher and response latencies were shorter in younger compared to older adults. Response latencies did not depend on accuracy in younger adults. In contrast, older adults showed longer response latencies in erroneous relative to correct responses. They tended to misperceive more responses than younger adults and showed a greater increase of misperceived errors from the easy to the difficult condition. However, the increase of uncertain choices with task difficulty was only found to be significant in younger adults.

The modulation of task difficulty led to different ERP patterns in both age groups, in that the ERN/Ne became larger and the CRN became smaller with increased task difficulty in younger adults, but not in older adults. This could be interpreted as a deficit to adjust performance monitoring according to task conditions and thereby, to task demands.

3.4 Study 3: Speeding up older adults: Age-effects on error processing in speed and accuracy conditions

The finding of normal error rates but longer response latencies in older compared to younger adults (Falkenstein et al., 2000; Falkenstein et al., 2001b; Nieuwenhuis et al., 2002) suggests a more conservative and controlled strategy in the older age group when performing a choice reaction time task. The aim to respond cautiously may be caused by a compromised representation of the correct response and/or a deficit to adapt to changing task demands. This experiment aimed at investigating whether age-related differences in performance monitoring are a consequence of these compensatory processes e.g., slower responses and the engagement of additional cognitive control. Thus, a modified flanker task with either accuracy or speed instruction was conducted in order to vary the demand of adaptation and the resistance to respond cautiously (Endrass, Schreiber, & Kathmann, 2012b). While compensatory processes should be maintained in the accuracy condition, time pressure in the speed condition should prevent behavioral compensation in the older age group. As a consequence, age differences were expected to increase in the speed condition since older adults should be less able to compensate for potential deficits.

Twenty-two older adults and 22 younger adults performed an arrow version of the flanker interference task (Eriksen & Eriksen, 1974; Kopp et al., 1996) with an instruction that either emphasized accuracy (accuracy condition) or speed (speed condition) in three blocks each. Subsequent to each error in the accuracy condition participants were informed about their erroneous response applying a visual feedback signal. When participants responded slower than an individually adapted response deadline in the speed condition a visual feedback advised them to respond faster in the following trial. Responses were registered with force-sensitive response devices to exclude a co-activation of partial error processing on correct trials.

ERN/Ne amplitudes were smaller in older compared to younger adults and this was more pronounced in the speed relative to the accuracy condition. CRN amplitudes did not differ with age. While the ERN/Ne was found to be larger than the CRN in younger adults, amplitudes were similar-sized in older adults. With regard to task instructions data showed an ERN/Ne reduction from the speed to the accuracy condition. This pattern was marginally more pronounced in the older age group. Only younger adults showed reduced CRN amplitudes in the speed compared to the accuracy condition.

Behavioral results revealed that both groups performed slower and more accurate in the accuracy relative to the speed condition. Overall, older adults committed fewer errors than younger adults, but this effect did not reach statistical significance. Older adults showed longer response latencies and this was more pronounced in correct trials. Noteworthy, response latencies on correct and incorrect responses did not differ between groups when comparing response latencies in the accuracy condition of younger adults with response latencies in the speed condition of older adults.

Older adults committed fewer errors than younger adults irrespective of task instruction. This appears to be only accomplished by the expense of slower responses. Hence, performance monitoring alterations in older adults (i.e., ERN/Ne attenuation) seem to be associated with deficits in behavioral task performance. This assumption is supported by the finding of a significantly reduced ERN/Ne in older adults when errors with similar response latencies were compared between age groups. The more pronounced ERN/Ne attenuation in the speed condition in older adults is probably caused by the force to overcome their cautious response strategy in favor of a more liberal strategy that decreased compensatory cognitive control mechanisms. The finding of a reduced dissociation between ERN/Ne and CRN amplitudes in older adults is assumed to be related to a deficit of the prefrontal cortex i.e., by a reduced modulation of monitoring activity or by deficits in error-specific processing.

4. Discussion

The aim of this thesis was to advance knowledge about ERN/Ne and CRN alterations with age. Specifically, these studies focused on the examination of potential compensatory strategies in the older age group and their implications for ERP results. Results indicated smaller ERN/Ne amplitudes and larger or similar-sized CRN amplitudes in older compared to younger adults. ERN/Ne and CRN amplitudes were less variable in the group of older compared to the group of younger adults and older adults revealed a reduced dissociation of

ERN/Ne and CRN amplitudes. All current studies found normal error rates but prolonged response times in older adults which is consistent with other studies (Band & Kok, 2000; Endrass et al., 2012b; Falkenstein et al., 2001b; Hoffmann & Falkenstein, 2011; Kolev et al., 2005; Mathalon et al., 2003a; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Schreiber et al., 2012; Schreiber et al., 2011). This behavioral finding suggests a more conservative and carful response strategy that probably has a compensatory function. Applying this strategy may be necessary to overcome a primary deficit in multiple cognitive domains that changes processes in cognitive control and to reach high performance (Braver & Barch, 2002; Treitz et al., 2007; Verhaeghen & Cerella, 2002; West, 1996). The use of this compensatory strategy presumably results in age-related ERP alterations that reflect the additional allocation of cognitive control in the older age group.

A candidate for this primary deficit in older adults is described in the dual mechanisms of control (DMC) framework (Braver, 2012). It is proposed that older adults have problems with the effective engagement of proactive control that requires the prediction of upcoming task demands and the maintenance of control over several trials (Braver, Grayson, & Burgess, 2007; Czernochowski, Nessler, & Friedman, 2010). As a consequence, they predominantly rely on reactive control mechanisms, which do not require sustaining control over extensive time periods. The need for upregulating reactive control is signaled when task demands are higher than anticipated and response conflict occurs (Braver & West, 2008). Younger adults are supposed to be able to recruit both proactive and reactive control when necessary, thereby adapting to the entire range of task demands. In contrast to younger adults, older adults may apply reactive control more often and under conditions with less task demands. Since proactive control and reactive control are assumed to be related to advantages and limitations, successful monitoring processes presumably depend on a mixture of both strategies. It is further proposed by Braver (2012) that the efficiency of proactive and reactive control can be measured by the amount of residual response conflict following decision reflected by CRN amplitudes. According to the DMC framework proactive control is associated with smaller CRN amplitudes than reactive control.

While the first study showed larger CRN amplitudes in older compared to younger adults (Schreiber et al., 2011) the two following studies (Endrass et al., 2012b; Schreiber et al., 2012) showed that age groups did not differ in the size of CRN amplitudes. According to the DMC framework, task demands in the first study allowed younger adults to prepare for the response that was required. Proactive control was recruited and CRN amplitudes remained small. In contrast, anticipation was unachievable for older adults, cognitive control was allocated at the time of response conflict detection and CRN amplitudes increased (Schreiber et al., 2011). The larger CRN in older compared to younger adults may therefore indicate that older adults recruit reactive control instead of proactive control like younger adults (Braver, 2012). This is confirmed during medium and high levels of task difficulty. Again, older adults were found to reveal larger CRN amplitudes than younger adults (Czernochowski et al., 2010; see also Maier et al., 2010). However, the second study revealed CRN amplitudes that neither differed in the easy nor in the difficult condition between younger and older adults even though error rates and thereby, task demands increased with the difficulty level in both age groups. But, while younger adults exhibited larger CRN amplitudes in the difficult compared to the easy condition, the CRN did not vary between difficulty levels in older adults (Schreiber et al., 2012). As claimed by the DMC framework this means that younger adults adjusted their strategy from proactive control in the easy condition to reactive control in the difficult condition. Conversely, older adults used the same strategy in the easy and in the difficult condition. This finding probably signals their deficit to adjust to changing task demands.

This interpretation is supported by modulations of the CRN in the first study (Schreiber et al., 2012) and in the third study (Endrass et al., 2012b). Younger adults had smaller CRN amplitudes for compatible trials than for incompatible trials whereas CRN amplitudes in older adults did not vary (Schreiber et al., 2011; see also Eppinger et al., 2007). Additionally, task instruction was found to affect CRN amplitudes in younger adults, i.e., the CRN was smaller under speed than under accuracy instruction. CRN amplitudes in older adults were not found to be affected by task instruction (Endrass et al., 2012b). This supports the assumption of changes in cognitive control processes with age. In particular, results show that older adults have deficits to flexibly adjust from proactive to reactive control and that they compensate for this deficit by a conservative response strategy. This is indicated by the finding of error rates that did not differ between age groups in the difficult condition (Schreiber et al., 2012) or in the speed condition (Endrass et al., 2012b) while response latencies were longer in older compared to younger adults and ERP amplitudes changed with age. In other words it could be speculated that older adults have deficits to adjust strategies at the level of cognitive control (i.e., they predominantly rely on reactive control), but at the behavioral level they are able to adjust strategies (i.e., they reduce response latencies to keep error rates low). This is supported by the existence of post-error slowing (Band & Kok, 2000; Nieuwenhuis et al., 2002; Schreiber et al., 2012) which is more likely an automatic and unconscious process, and which is usually referred to strategic control adjustments towards a more conservative response threshold (Notebaert et al., 2009).

Even though Braver (2012) did not formulate predictions about the ERN/Ne component within the DMC framework it can be considered that the less flexible adaptation of monitoring processes in older adults is also associated with alterations in error monitoring as reflected by the ERN/Ne. The ERN/Ne was found to be reduced in older compared to younger adults (Band & Kok, 2000; Falkenstein et al., 2001b; Mathalon et al., 2003a; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Themanson et al., 2006) and it seems to be a robust finding in choice response conflict tasks. This is supported by studies showing reduced ERN/Ne amplitudes in the older age group when error rates were higher (Mathewson et al., 2005), smaller (Czernochowski et al., 2010; Nessler et al., 2007; Nieuwenhuis et al., 2002; Schreiber et al., 2012; Schreiber et al., 2011), or similar (Beste et al., 2009; Endrass et al., 2012b; Falkenstein et al., 2001b; Kolev et al., 2005; Mathalon et al., 2003a), and when post-error slowing was larger in older compared to younger adults (Backman et al., 2000; Band et al., 2002; Schreiber et al., 2012), or absent (Endrass et al., 2012b; Schreiber et al., 2011). However, in the second study the smaller ERN/Ne in older compared to younger adults was exclusively obtained in the easy condition (Schreiber et al., 2012). This is in line with previous studies indicating that age-related changes in ERN/Ne amplitudes vary with task demands: When a clear representation of the correct response was built, the ERN/Ne was attenuated in older compared to younger adults (Band & Kok, 2000; Band et al., 2002; Endrass et al., 2012b; Falkenstein et al., 2001b; Mathalon et al., 2003a; Mathewson et al., 2005; Nieuwenhuis et al., 2002; Schreiber et al., 2011; Themanson et al., 2006). When a gradual development of the correct response representation was required in learning tasks the ERN/Ne attenuation in older adults was not observed (Eppinger et al., 2008; Pietschmann et al., 2011a; Pietschmann et al., 2011b; Pietschmann et al., 2008). Thus, the absence of age-related ERN/Ne differences in the difficult condition was presumably caused by weakened representations of the correct response (Schreiber et al., 2012).

Similar to the CRN, the ERN/Ne was not only observed to be altered in the absolute size between younger and older adults but also in the variation with changing task demands. Contrary to younger adults, older adults did not show an ERN/Ne decrease from the easy to the difficult condition (Schreiber et al., 2012) indicating that error detection function did not differ between the two conditions. The absence of an ERN/Ne modulation with task difficulty (Schreiber et al., 2012) can be interpreted as a deficit in building a representation of the correct response although conditions would allow it. At the behavioral level, older adults showed a stronger increase of error misperception rates from the easy to the difficult condition and uncertainty ratings were less related to task difficulty compared to younger adults. This may indicate that conscious monitoring of own actions is less determined by the objective likelihood of errors in the older age group. In contrast to the second study, older adults showed ERN/Ne variations with task demands. ERN/Ne amplitudes were smaller in the speed than in the accuracy condition in both younger and older adults. The ERN/Ne reduction was even more pronounced in older adults. The finding of faster and less accurate responses in older adults indicates reduced compensatory cognitive control under speed instruction. Hence, performance monitoring deficits were amplified when older adults were forced to focus on speed and changed their cautious for a more liberal response strategy.

Alternatively, it was suggested that the reduction of flexible adaptation of monitoring processes to changing task demands is caused by a compromised representation of the actually relevant task context in older adults (Eppinger et al., 2007). This may lead to the absence of expectancies about the appropriate response strategy in the next trial. Hence, expectancies could not be violated and the need for upregulating cognitive control was not represented (Bartholow et al., 2005). Consistently, it was postulated that older adults elicited “relatively undifferentiated executive processes” on trials with low or high demands whereas younger adults seem to respond in accordance with the level of cognitive demands (Friedman, Nessler, Cycowicz, & Horton, 2009). Further, older adults are able to adapt to changing task demands under certain conditions (Friedman et al., 2009), which could be due to a correct representation of the relevant task context. This could explain why some studies found a similar pattern of CRN variations with trial compatibility in younger and older adults (Friedman et al., 2009; Nessler et al., 2007) and some studies did not (Eppinger et al., 2007; Kray et al., 2005; Schreiber et al., 2011).

To summarize, the potential deficit to use a successful combination of both proactive and reactive control presumably causes the need for a compensatory strategy in older adults. This strategy seems to be quite effective as indicated by similar accuracy in younger and older adults. But, it also leads to performance monitoring processes that are less flexible as reflected by reduced variability of ERN/Ne and CRN amplitudes in older adults.

5. Conclusion, limitations and future directions

In my thesis I focused on behavioral and ERP correlates of performance monitoring and their alterations with age. The ERN/Ne was found to be reduced in older compared to younger adults. It decreased with task difficulty in the group of younger adults, and with the focus on speed in both age groups. The CRN was found to be larger in older compared to younger adults or not affected by age, respectively. CRN amplitudes did not vary with trial compatibility, with task difficulty, and with task instruction in the group of older adults. Conversely, younger adults showed a smaller CRN for compatible compared to incompatible trials, in the easy compared to the difficult condition, and in the speed compared to the accuracy condition. In contrast to younger adults, older adults did not provide a dissociation of ERN/Ne and CRN amplitudes. Behaviorally, older adults performed more accurate and slower compared to younger adults. They were less successful in the detection of errors and tended to misperceive more responses than younger adults.

The pattern of fewer errors and slower responses indicates a cautious and conservative response strategy in older adults that is interpreted to be a compensation of the deficit to successful combine proactive and reactive control. This compensatory strategy is assumed to affect ERN/Ne and CRN amplitudes. Alternatively, other accounts proposed that ERN/Ne and CRN reflect a general mismatch signal that either indicates errors or the need for strategy adjustment (Bartholow et al., 2005). Consistently, it is suggested that both components share a common process that reflects general monitoring function. The absence of CRN variations with trial compatibility, task difficulty, or task instruction in the older age group supports the notion of a less flexible monitoring function and adaptation to changes in task demands.

The registration of trial-by-trial response accuracy ratings and partial responses using force-sensitive response devices enabled us to identify correct responses that are consciously perceived to be correct and correct responses with previous incorrect activation. The assumption of the CRN to be an artifact caused by erroneous activity under response threshold (Coles et al., 2001) or to be a correlate of response uncertainty (Pailing & Segalowitz, 2004a; Scheffers & Coles, 2000) could therefore be eliminated. To separate the effect of task difficulty in the second study it would have been very informative to assess ERN/Ne amplitudes only from subjectively perceived error trials. But, the number of subjectively perceived error trials was too low in some participants and all error trials had to be included into analyses (Schreiber et al., 2012). A potential limitation is that age-related ERP alterations were confounded by behavioral differences (Olvet & Hajcak, 2008). Therefore analyses of the first study were repeated with a subsample of trials that was matched between age groups. As a result, error rates and response latencies did not differ significantly between younger and older adults and ERP findings did not change (Schreiber et al., 2011). Another limitation is given by Maier et al. (2010) who argued that the comparison of response-locked ERPs from conditions with different response latencies could give misleading information due to different stimulus-locked potentials.

Future research will be needed to answer the question of whether ERN/Ne and CRN are independent or share common processes. If both components include common and independent processes it would be interesting to study how these processes are (differentially) affected by age. Findings of age differences in CRN amplitudes are still inconsistent. The CRN seems to depend on task difficulty and/or task demands (e.g., flanker go nogo: Beste et al., 2009; two-choice reaction time task: Nessler et al., 2007; visual size discrimination task: Schreiber et al., 2012) and sample characteristics (i.e., mean age of older adults varies between 58 and 75 years; Falkenstein et al., 2001b; Mathalon et al., 2003a). The inconsistency and the unresolved functional role of the CRN impede the explanation of age-related CRN alterations. Hence, studies need to examine specific task characteristics and sample characteristics that are responsible for different age effects. The ability to increase cognitive control and to compensate for executive deficits may be associated with high education levels in older adults. Samples of various mean ages (young-old vs. old-old) are already been found to affect results (Ferrandez & Pouthas, 2001). Assuming that age-related ERP differences are caused by older adults' tendency to compensate for the deficit to successful combine proactive and reactive control, examinations are needed that bring them to overcome their cautious response strategy.

Given the aging of our population and the significance of performance monitoring in daily live, it is critically important to proceed research examining performance monitoring alterations with age. This will lay essential groundwork for future investigations focusing on goal-directed behavior and the flexible adaptation to changing demands in the older age group.

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7. Scientific Papers

Study 1

Schreiber, M., Pietschmann, M., Kathmann, N., & Endrass, T. (2011). ERP correlates of performance monitoring in elderly. *Brain and Cognition, 76*(1), 131-139.

Study 2

Schreiber, M., Endrass, T., Weigand, A., & Kathmann, N. (2012). Age- effects on adjustments of performance monitoring to task difficulty. *Journal of Psychophysiology, 26*(4), 145-153.

Study 3

Endrass, T., Schreiber, M., & Kathmann, N. (2012). Speeding up older adults: Age-effects on error processing in speed and accuracy conditions. *Biological Psychology, 89*(2), 426-432.